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# Predicting the invasion range for a highly polyphagous and widespread forest herbivore

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## Abstract

Here we compare the environmental niche of a highly polyphagous forest Lepidoptera species, the winter moth (*Operophtera brumata*), in its native and invaded range. During the last 90 years, this European tree folivore has invaded North America in at least three regions and exhibited eruptive population behavior in both its native and invaded range. Despite its importance as both a forest and agricultural pest, neither the potential extent of this species' invaded range nor the geographic source of invading populations from its native range are known. Here we fit a climatic niche model, based on the MaxEnt algorithm, to historical records of winter moth occurrence in its native range and compare predictions of suitable distributions to records from the invaded range. We modeled this distribution using three spatial bins to overcome sampling bias for data obtained from public databases and averaged the multi-continental suitable habitat prediction. Results indicate that this species is distributed across a wide range of climates in its native range but occupies a narrower range in its invaded habitat. Furthermore, the lack of a close fit between climatic conditions in parts of its invaded range and its known native range suggests the possibility that this species has adapted to new climatic conditions during the invasion process. These models can be used to predict suitable habitats for winter moth invasions worldwide and to gain insight into possible origins of North American populations.

## Keywords

bioclimatic modelling, biological invasions, climatic envelope, geographical distribution, invasive alien species, range projection, species distribution models

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## Introduction

With heightened awareness of the damage caused by biological invasions, biosecurity programs take on increasing importance for preventing new invasions (Hulme 2009). Risk assessment plays a key role in biosecurity programs, providing information on likely invasion success and impacts of species, and is used to prioritize preventative measures (Hayes 2003). A crucial component of the risk assessment process is mapping the potential range of a species should it become established (Venette et al. 2010). Knowledge of the potential geographical distribution of a candidate invasive species can guide implementation of both pre- and post-border biosecurity activities such as surveillance.

Understanding and quantifying the ecological niche of a species in its native range can be used to predict its potential distribution in a novel environment. Ecological niche models use occurrence data and environmental variables to predict habitat suitability (Guisan and Zimmermann 2000). These models typically use available species occurrence records to quantify the association of a species' distribution with various components of its habitat such as climate. Ecological niche models assume that a species is well adapted to present climatic conditions and this acclimation assumption is carried into future distribution forecasts. For practicality, these models typically ignore the effects of biotic interactions which may limit a species' potential distribution, and thus are expressed as a realized niche. Application of ecological niche models to predict an invading species future range assumes that successful invasion of novel environments requires similarly matched climates between the native and novel regions (Panetta and Mitchell 1991).

Unfortunately, systematic surveys for most species throughout their ranges are often impractical, though a wealth of distribution information resides in global databases and museum collections worldwide. These datasets, such as the Global Biodiversity Information Facility (GBIF, GBIF.org 2018), assemble occurrence records from many different sources; however, the intensity of sampling behind these records often contains a sampling bias where more records exist in certain areas (such as near research facilities or locations with extensive sampling by hobbyists).

A number of methods can be applied to limit this spatial bias. One method of accounting for sampling bias is to use frequencies of background occurrence records of a conspecific species or an entire genus, often referred to as target group background bias records, as proxies for sampling effort (Yates et al. 2010). Another method involves spatially filtering the occurrence records to remove records at distances greater than the resolution of cells in the environmental layers (Aiello-Lammens et al. 2015; Boria et al. 2014; Hijmans 2012; Kramer-Schadt et al. 2013; Pearson et al. 2007; Veloz 2009). Occurrence records can also be thinned based on their environmental/climatic values, discarding repetitive occurrences in similar climatic conditions (Varela et al. 2014), or records can be filtered geographically, splitting occurrence records into geographic bins (Jiménez-Valverde et al. 2011; Radosavljevic and Anderson 2014).

This study focuses the use of ecological niche models for predicting the potential distribution of the winter moth, *Operophtera brumata*. The native distribution of this

species ranges widely through most of Europe (Kozhanchikov 1950) (Fig. 1). Furthermore, larvae of this species are known to have an extremely broad host range, feeding on the foliage of a wide variety of broadleaf trees and occasionally on certain conifer species (Wint 1983). Recurrent outbreaks of this insect occur in several regions of its native range, especially in mountain birch (*Betula pubescence*) forests in Fennoscandia (Jepsen et al. 2008), but also on other hosts, such as Sitka spruce (*Picea sitchensis*) planted in the British Isles (Stoakley 1985; Watt and McFarlane 1991) and even on heather (*Calluna vulgaris*) in Scotland (Kerslake et al. 1996).

Non-native populations of the species exist in portions of North America with alien populations established in Nova Scotia, the Pacific Northwest, and New England (Fig. 1). Winter moth was first accidentally introduced to Nova Scotia in the 1930s (Hawboldt and Cuming 1950), Oregon in the 1950s (Kimberling and Miller 1988), near Vancouver, British Columbia around 1970 (Gillespie et al. 1978), and eastern Massachusetts in the 1990s (Elkinton et al. 2010). It is unknown whether these represent separate introductions from the native range or a single invasion that has spawned several secondary introductions. Following the initial establishment of each of these populations there was some initial range expansion, though in each case, spread may

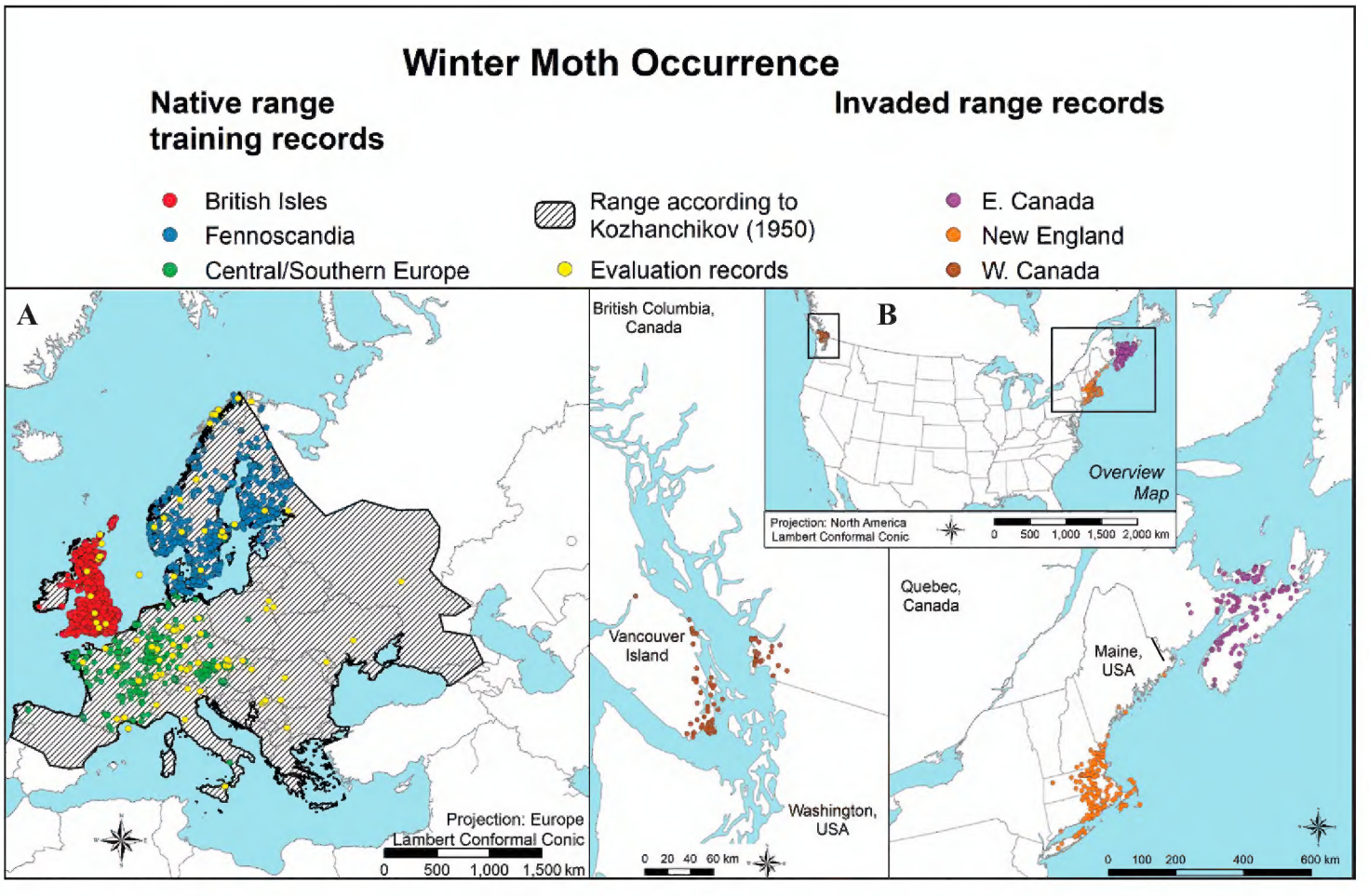


**Figure 1. A** map showing the distribution of the native range for winter moth (Operophtera brumata), recreated from Kozhanchikov (1950), as well as native winter moth occurrence records used as training records – colored according to three geographic filters (British Isles in red, Fennoscandia in blue and Central/Southern Europe in green) and evaluation records shown in yellow **B** map of North American records reflecting the invaded range separated into three geographic regions (western Canada in brown, New England in orange and eastern Canada in violet).

have been limited by climatic conditions, introduction of biological control agents, and/or by hybridization with the native congener, Bruce spanworm, *O. bruceata* (Elkinton et al. 2010).

The objective of this study was to fit ecological niche models based on winter moth occurrence records from its native range in order to predict the potential invaded range of this species. Furthermore, as there is much uncertainty about where in Europe the non-native populations of winter moth originated from (Andersen et al. 2017; Elkinton et al. 2010; Gwiazdowski et al. 2013), we use geographic filtering to compare the climatic suitability of different potential source populations to each of the invaded North American populations. We then comment on the utility of geographic filtering to reduce sample bias in datasets based on public records.

## Methods

### Modelling approach

The winter moth's climatic niche was quantified using the machine learning algorithm, MaxEnt v. 3.4.1 (Phillips et al. 2006), using presence-only data for this species. MaxEnt uses both distribution information and environmental variables to predict potential areas of distribution for a species. It provides an estimated likelihood for a species range that is near uniform and still subject to environmental confines (Elith et al. 2011). MaxEnt, the most widely used species niche and distribution modelling algorithm (Fourcade et al. 2014), is efficient for complex interactions between response and predictor variables with little sensitivity to small sample sizes. However, difficulties in accuracy arise when modelling generalist or widespread species (Connor et al. 2018; Jiménez-Valverde et al. 2008; Luoto et al. 2005; Marmion et al. 2009; Segurado and Araujo 2004).

### Occurrence records

Presence-only distribution data were assembled from various sources: GBIF (www.GBIF.org, taxon key = 1972449), Barcode Of Life Database (BoldData, www.barcodinglife.org), Canadian Forest Invasive Alien Species (CanFIAS, www.exoticpests.gc.ca) database, Elkinton et al. (2010), Andersen et al. (2017), and Tenow et al. (2013). These records were cleaned and separated into two subsets – all of the GBIF records were placed into a training dataset (n = 4151), while records from BoldData, CanFIAS, Elkinton, Andersen and Tenow were separated into a testing dataset (n = 518). Records from the training dataset, consisting of occurrence records for winter moth in the GBIF database, were downloaded on November 29, 2018 using the dismo package in R (Hijmans et al. 2017) and the gbif function. Both training and testing records were cleaned to remove any records where either the latitude or longitude coordinates were missing. Additionally, these records were filtered temporally,

keeping only those records between 1970 and 2010, to best align with the environmental layers while maintaining a large sample size. Next, these records were visualized in ArcMap (ESRI 2017) to group locations (Fig. 1) into three regions for native range records: the British Isles (n = 2846), Fennoscandia (n = 894), and Central/Southern Europe (n = 398); and three regions for invaded range records (n = 103): Western Canada, Eastern Canada and New England. The three native range regions were arbitrarily selected as geographically isolated areas, each with unique densities of occurrence records. The three invaded range regions were selected because they represent isolated ranges, though there is a small coastal area where the Eastern Canada and New England regions are contiguous (Fig. 1). Finally, only unique records were kept – using the delete identical tool with the advanced license of ArcMap. These cleaned records were re-projected into the World Molliweide projection, to match that of the environmental layers, and the latitude and longitude were recalculated before creating a CSV file to be used in MaxEnt.

## Sampling bias

Accurate application of MaxEnt necessitates accounting for the effects of geographical sampling bias in locations of occurrence data. Use of occurrence data sets that are spatially biased can result in over-representation of certain environmental features prevalent in more intensively surveyed areas (Phillips et al. 2009). If the sampling effort is known, it can be included in the model calibration to correct for sampling bias (Anderson 2012; Phillips et al. 2009). However, this is rarely the case especially when using museum records from databases, such as GBIF.

We focused our analysis on geographic filtering or splitting of the data into bins to overcome sampling bias. Due to the winter moth's extensive geographical range and the comparatively high density of records in the United Kingdom compared to Central/Southern Europe, we selected to split location records from the native range into three geographical bins: the British Isles, Fennoscandia, and Central/Southern Europe (Fig. 1) as the simplest method for handling sampling bias.

## Environmental variables

Environmental variables included in the model were selected from WorldClim 10 minute resolution variables (Fick and Hijmans 2017). WorldClim version 2 includes gridded values for 19 bioclimatic variables derived from temperature and precipitation measurements spanning 1970–2000 collected from a global network of meteorological stations. All environmental variables were resampled in R using the bilinear method to a 25 km cell size in the Mollweide projection, which maintains equal areas – an assumption that is required for MaxEnt models (Elith et al. 2011). We chose to use the following temperature variables that are likely to be of biological importance, BIO1–4,

**Table 1.** WorldClim v.2 bioclimatic variables included in the model, and their descriptions.

| Variable | Description |
|---|---|
| BIO1 | Annual Mean Temperature (°C) |
| BIO2 | Mean Diurnal Range (Mean of monthly (max temp – min temp)) (°C) |
| BIO3 | Isothermality ((BIO2/BIO7) * 100) |
| BIO4 | Temperature Seasonality (standard deviation *100) |
| BIO6 | Min Temperature of Coldest Month (°C) |
| BIO7 | Temperature Annual Range (BIO5-BIO6) (°C) |
| BIO10 | Mean Temperature of Warmest Quarter (°C) |
| BIO11 | Mean Temperature of Coldest Quarter (°C) |
| BIO14 | Precipitation of Driest Month (mm) |

6–7, 10–11 and 14 (Table 1). Insects are ectotherms and therefore their development is sensitive to accumulated degree days as well as to extreme temperatures (Battisti and Larsson 2015). For this reason, we concluded that temperature would be more likely to influence the distribution of winter moth than precipitation, but also identified drought as possibly affecting the pupal stage which reside in the top layer of the soil throughout the summer and early autumn, hence the inclusion of BIO14. Given the polyphagous nature of winter moth larvae, we expected that suitable host plants are present in most locations of the native and invaded ranges and therefore we did not include any variable describing vegetation as predictive environmental variables.

## Model parameters

We fit MaxEnt models using the following adjustments to default settings. We generated response curves and jackknife statistics to measure variable importance. Samples files consisted of training datasets for each spatial bin. Environmental layers were clipped to a 400 km buffer around each sample file. The projection layers directory consisted of environmental variables clipped to latitudes above 20°N. The algorithm created 100 replicate models for cross validation. The test sample file was the corresponding testing dataset, the maximum iterations was changed to 5000 for reaching algorithm optimization. A statistical analysis was performed on data extrapolated from each model run, using the receiver operating characteristic (ROC) plot to evaluate model performance. The area under the curve (AUC) of an ROC curve ranges in values from 0 to 1 (Fielding and Bell 1997) with a value of 0.5 indicating that the model performed as good as random and a value of 1 indicates the model has perfect discrimination.

Selection of an appropriate background extent during ecological niche modeling is often overlooked. If the considered extent is too narrow to accurately represent the potential movement of a species over time, the importance of climatic variables in demarcating a species' distribution may be underestimated (Barve et al. 2011). We chose a buffer distance of 400 km, roughly the distance between the Nova Scotia population and the Massachusetts population. However, this distance is much larger than the likely generational winter moth maximum dispersal distance; windborne first

instar larvae are known to balloon 50 m (Edland 1971; Huntley et al. 1995) and adult females are incapable of flight.

Model complexity can be varied by altering the regularization parameter; this parameter reduces omission rates. After running the models with regularization values of 0.1, 1 and 3, we chose to use a regularization parameter of 3 to avoid over-fitting our distribution model.

## Analyzing the climatic niche

Ridgeline plots of the distribution of environmental variables (BIO 1–4, 6–7, 10–11, 14) among samples were created to further identify differences and similarities in the abiotic niche for each spatial bin from the native versus novel locales. Next, principal components analysis was applied to the nine environmental variables for the pooled occurrence records (both native and invaded ranges) and scores for the first two principal components were plotted separately for each spatial bin (British Isles, Fennoscandia, and Central/Southern Europe, Western Canada, Eastern Canada and New England) in order to discern climatic similarities and differences among regions. ArcMap was used to create a 15 km fishnet of points for the entire study area, which extends 400 km beyond sites of winter moth occurrences in both the native and novel ranges. Next, WorldClim layers were speared to assign their values to each point location. Additionally, cells were coded based on their geographic location (spatial bin) and if within 15 km of a winter moth occurrence. These occurrence data were then exported to R and principal components analyzed with the 'prcomp' function in the base R language.

## Distribution modelling

Three different MaxEnt models, one fit to occurrence data from each of the three geographical bins of the native range, were used to predict probabilities of suitable habitat for winter moth in North America. These three model predictions were then averaged to create a combined model and these probabilities were classified into three levels of habitat suitability

MaxEnt output consist of continuous probability values ranging from 0 (unsuitable habitat) to 1 (suitable habitat). MaxEnt output provides the modeler with 11 thresholds to choose from when converting the suitability map to a binary map, all of these thresholds provide a balance between commission and omission rates (Fielding and Bell 1997; Phillips et al. 2017). Model outputs were converted to classified suitability maps. To do this we employed MaxEnt's 'balance' threshold which minimizes 6.00 * training omission rate + 0.04 * cumulative threshold + 1.60 * fractional predicted area. Values below this threshold were dropped and a composite map was created, averaging across predicted probabilities from models derived from each of the three geographical bins in the native range.

## Results

### Predictions based on native range occurrences

All three models fit to native range records from spatial bins (Fig. 2) performed better than random (Table 2; British Isles AUC = 0.795, Fennoscandia AUC = 0.75, Central/Southern Europe AUC = 0.816). Predictions of suitable winter moth habitat in Europe and North America based on averaging probabilities from the three different models are shown in Fig. 3. The predicted distribution in Europe based on the average of the three models mostly corresponds well with the extent of the distribution map from Kozhanchikov (1950) (Fig. 1). However, the predicted area of suitable habitat extends beyond the eastern boundary of occurrence records into the Carpathian and Caucasus Mountain ranges (Fig. 3). The predicted distribution in North America correctly predicts the winter moth distribution in western Canada, but also predicts extensive areas of suitable habitat north of the invaded range, along the coast of the Cordillera region in Canada and into the Pacific Mountain System of Alaska including the Alaska Peninsula. The prediction for suitable habitat in eastern North America includes a small portion of Nova Scotia, but overall misses most of the Winter Moth's current eastern North American range and instead predicts moderately suitable habitat farther north in eastern Newfoundland. Areas of low habitat suitability in North America are also predicted in the Canadian Rockies, Northern Idaho, Western Montana and the Appalachian Mountains.

### Comparison of predicted distributions based on regional bins

Predicted suitable habitat in North America varies among models fit to different geographic bins of native occurrence records (Fig. 2). Models fit to occurrences in the British Isles identified only a small region of suitable habitat in North America, in British Columbia along the North, South and West coasts of Vancouver Island, as well as in Naikoon Provincial Park on Graham Island and in Washington in the San Juan Islands, Fidalgo Island, Whidbey Island and along the northern coast of the Olympic Peninsula from Port Townsend to Neah Bay. Models fit to occurrences in Fennoscandia predicted the greatest amount of suitable habitat in North America, including the entire coast of British Columbia and the southern coast of Alaska from the Prince of Wales Island to the Alaska Peninsula in Western North America and in the East suitable habitat is found throughout Newfoundland and in spots along the southern and southwestern coast of Nova Scotia and on Cape Breton Island. The models fit to occurrences in Central/Southern Europe found moderate to low suitability along the western coast of British Columbia north to the Alaska Peninsula with a localized region of moderately high suitability in the vicinity of Vancouver in Western North America, low predicted suitability along the southeastern coast of Newfoundland, moderate to low suitability along the southern coast of Nova Scotia, as well as low suitability in the Appalachian

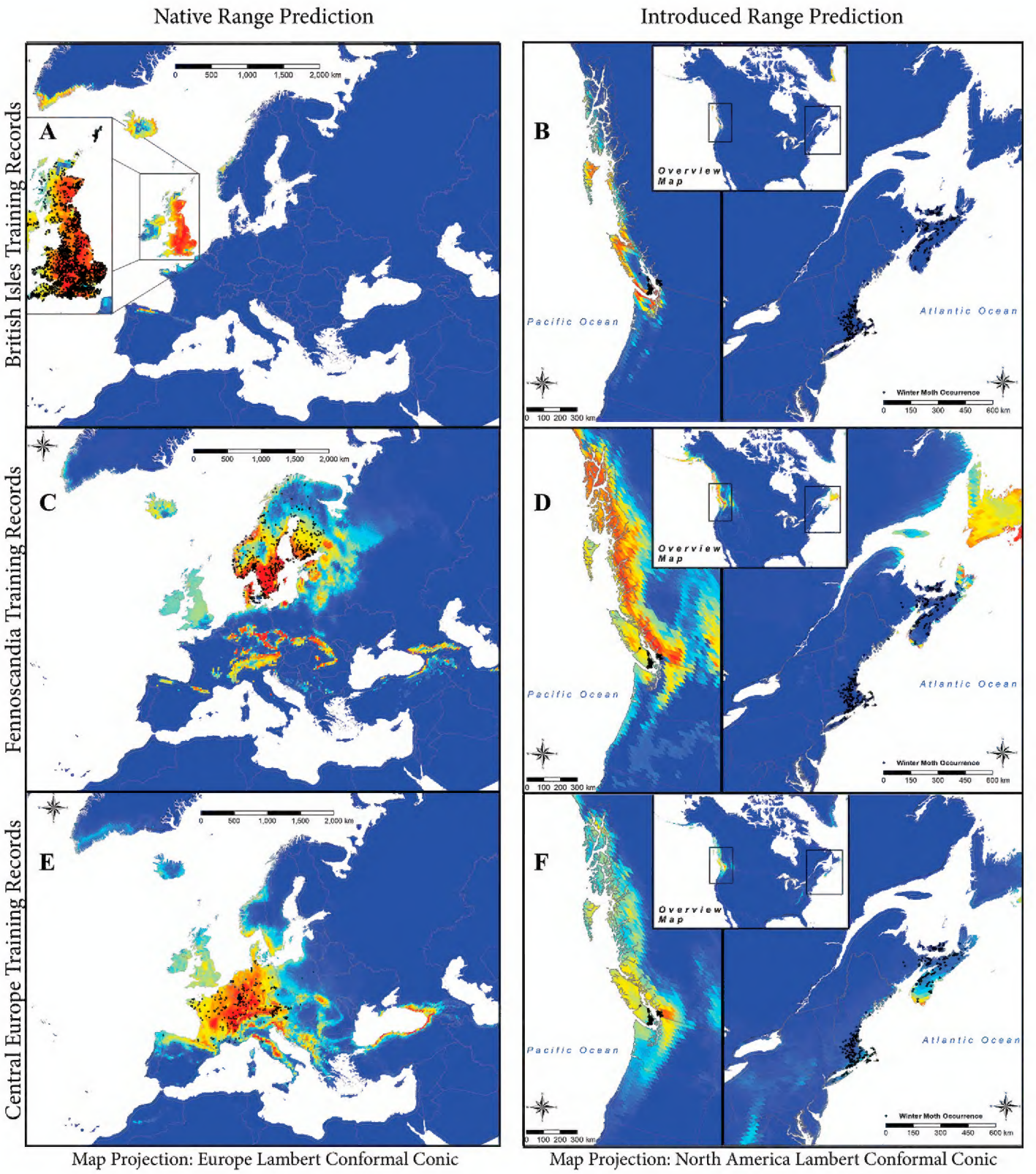


**Figure 2.** Model predictions for each spatial bin in the winter moth native range. The column on the left shows the winter moth training records (shown as black dots) used to make the predictions for suitable habitat in the native range and the column on the right shows the suitable habitat prediction for the invaded range. The prediction is shown from blue (being less suitable) to red (being most suitable).

Mountains and along the New England coast with Cape Cod and Nantucket Island displaying moderately suitable habitat. Models based on the different geographic bins highlight varying degrees of suitable habitat in the vicinity of invaded regions of Vancouver and Vancouver Island; however, the predictions of suitable habitat in Eastern North America were generally not as congruous with the invaded areas with very little overlap between models.

**Table 2.** Model results for each spatial bin. Percent contribution of environmental variables are in bold for those variables that showed the highest model gain in isolation; values highlighted in gray represent the most information not present in other variables, and * denotes balance threshold used for classified maps which seeks to balance training omission, predicted area and threshold value cloglog threshold.

| Winter Moth Region | sample size | threshold values* | AUC | % Contribution of Environmental Variables | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | BIO1 | BIO2 | BIO3 | BIO4 | BIO6 | BIO7 | BIO10 | BIO11 | BIO14 |
| British Isles | 381 | 0.1432 | 0.795 | 1.1 | 0.6 | 9.3 | **42.8** | 14.5 | 0.1 | 29.5 | 0.4 | 1.7 |
| Fennoscandia | 379 | 0.1132 | 0.75 | 5.1 | 6 | 5.6 | 0.7 | 16.4 | 0.3 | **47.1** | 18.7 | 0.1 |
| Interior Europe | 224 | 0.0806 | 0.816 | 1.4 | 0.6 | 7 | 2.4 | 1.1 | 33.7 | 6.2 | 2.1 | **45.6** |
| **Model Averages** | | | | 2.5 | 2.4 | 7.3 | 15.3 | 10.7 | 11.4 | 27.6 | 7.1 | 15.8 |

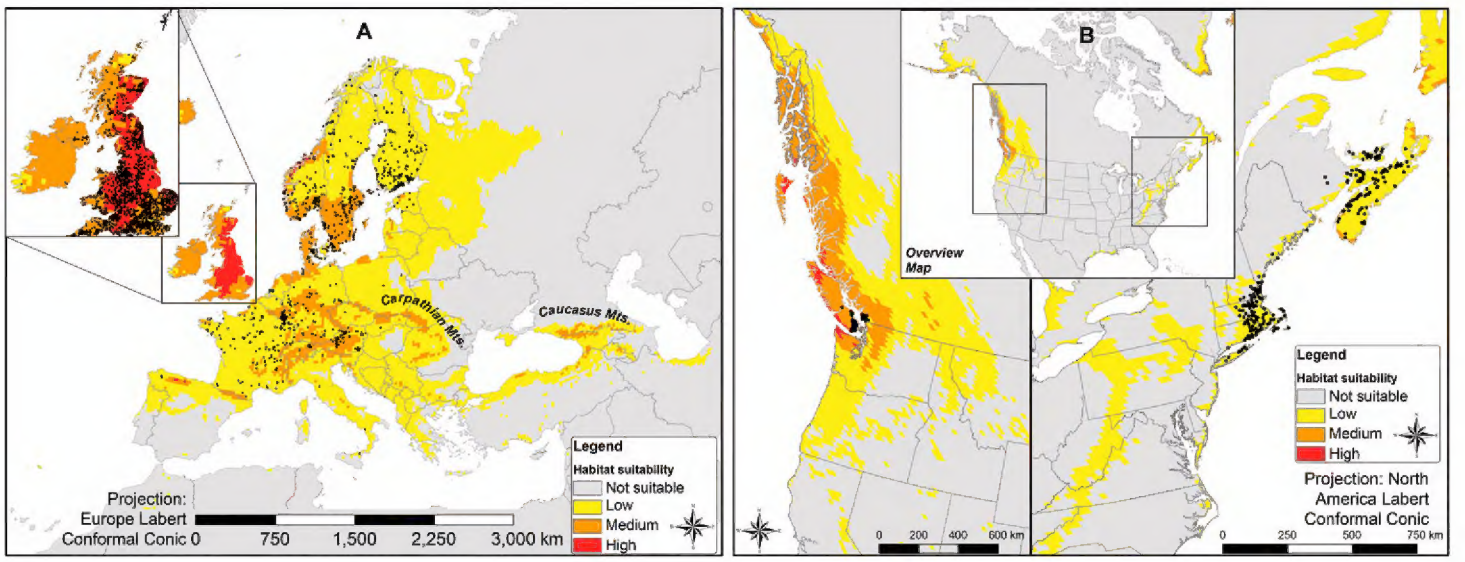


**Figure 3.** Predicted suitable habitat in native range (panel **A**) and invaded range (panel **B**) with occurrence records (shown as black dots), this reclassified map is based on the averaged prediction for three spatial bins in the native range. Probabilities falling below balance threshold values shown in Table 2 for each of the three models were classified as "not suitable". Probabilities ≤ 0.25 were classified as "low suitability", values > 0.25 but ≤ 0.5 were classified as "medium suitability" and values > 0.5 were considered "high suitability".

## Analysis of environmental variables

Environmental variables contributed differently for each spatial bin (Table 2). Jackknife analyses indicated that the relative contribution of different environmental variables differed considerably among the three models. Temperature seasonality (BIO 4) is the environmental variable that contributed the most to the model fit from occurrences from the British Isles. In the model fit to Central/Southern Europe occurrences, precipitation during the driest month (BIO 14) contributed the most to this model. Mean temperature of the warmest quarter (BIO 10) contributed most to the model fit from Fennoscandia occurrences. When averaging model results for variable contribution across spatial bins, the environmental variables contributing the most influence in the native range are BIO 10, 14, 4, 7 and 6.

While there was considerable overlap in the distribution of climatic variables between the native and invaded ranges, ridgeline plots highlight the variation among populations (Fig. 4). These plots highlight the similarities between the New England

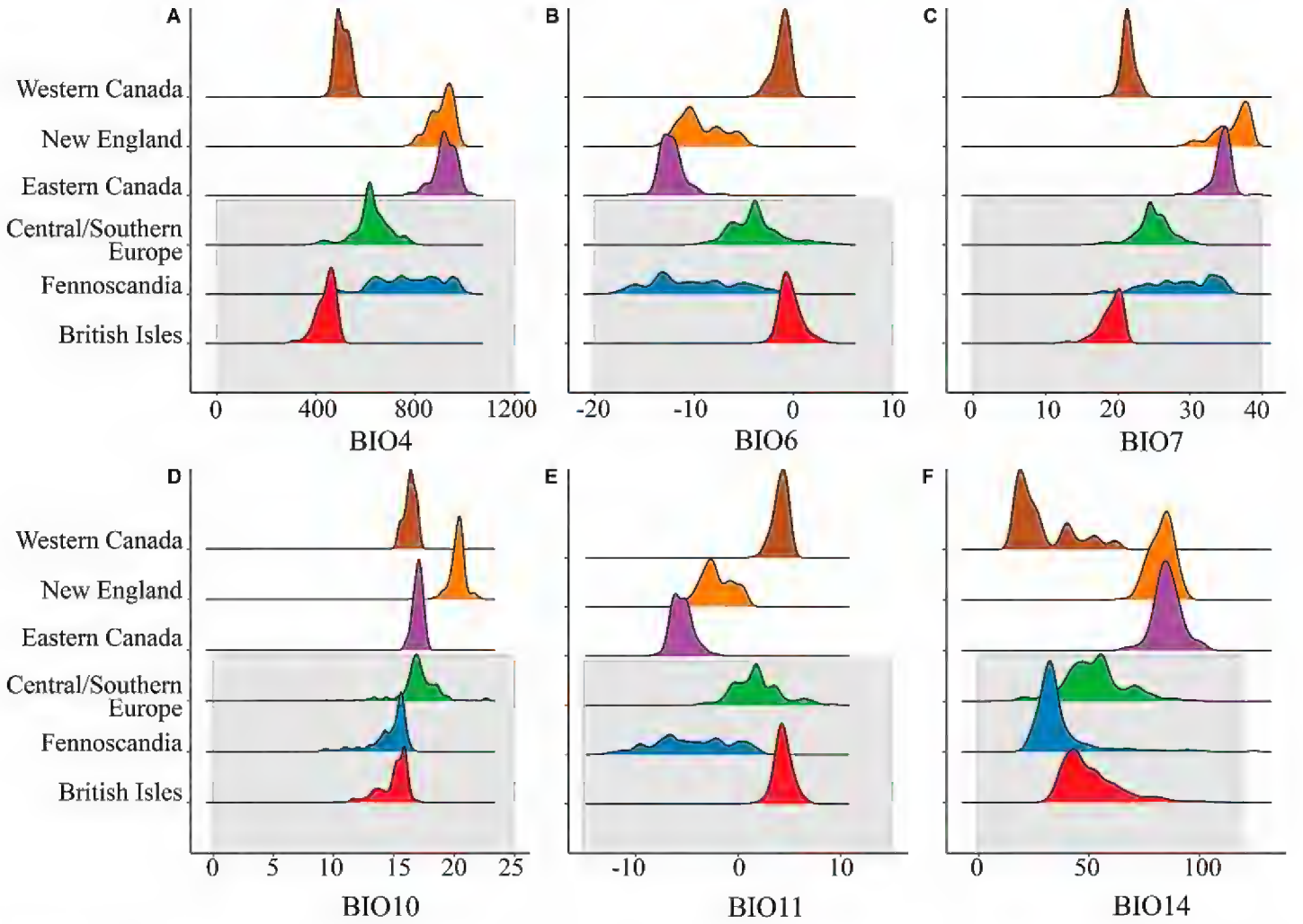


**Figure 4.** Distribution of bioclimatic variables among occurences within various geographic bins. Gray shading represents winter moth records in the native range. Bioclimatic variables found to contribute the most for each model area shown here, panel **A** shows BIO4 (temperature seasonality, standard deviation *100), panel **B** shows BIO6 (minimum temperature of coldest month, °*C*), panel **C** shows BIO7 (temperature annual range, °*C*), pancel **D** shows BIO10 (mean temperature of warmest quarter, °*C*), panel **E** shows BIO 11 (mean temperature of coldest quarter, °*C*) and panel **F** shows BIO 14 (precipitation of driest month, *mm*).

region and Eastern Canada, with New England showing more variability in BIO 6, 7, 10 and 11. When comparing Eastern Canada to the native regions, more climatic values overlap with the Fennoscandia region (BIO 4, 6, 7 and 11) but values of only two variables (BIO 10 and 14) overlap with the Central/Southern Europe region. Values of climatic variables from the New England region overlap with the distribution of values in both Fennoscandia and Central/Southern Europe. The Western Canada region seems most similar to the British Isles across most climatic variables.

Finally, we used principal components analysis to compare the environmental niche at occurrence sites for winter moth in each geographic region (Fig. 5). We analyzed the same climatic variables used in the MaxEnt models (BIO 1–4, 6–7, 10–11 and 14). The first axis generally corresponded to values of BIO3, BIO4, BIO6, BIO7, BIO11 and BIO14 while the second axis was most strongly related to values of BIO10, but also corresponded to values of BIO1 and BIO2. The three native range regions and three invaded regions were generally segregated in the space defined by these two axes. However, there was considerable overlap in the distribution of Central/Southern Europe with western

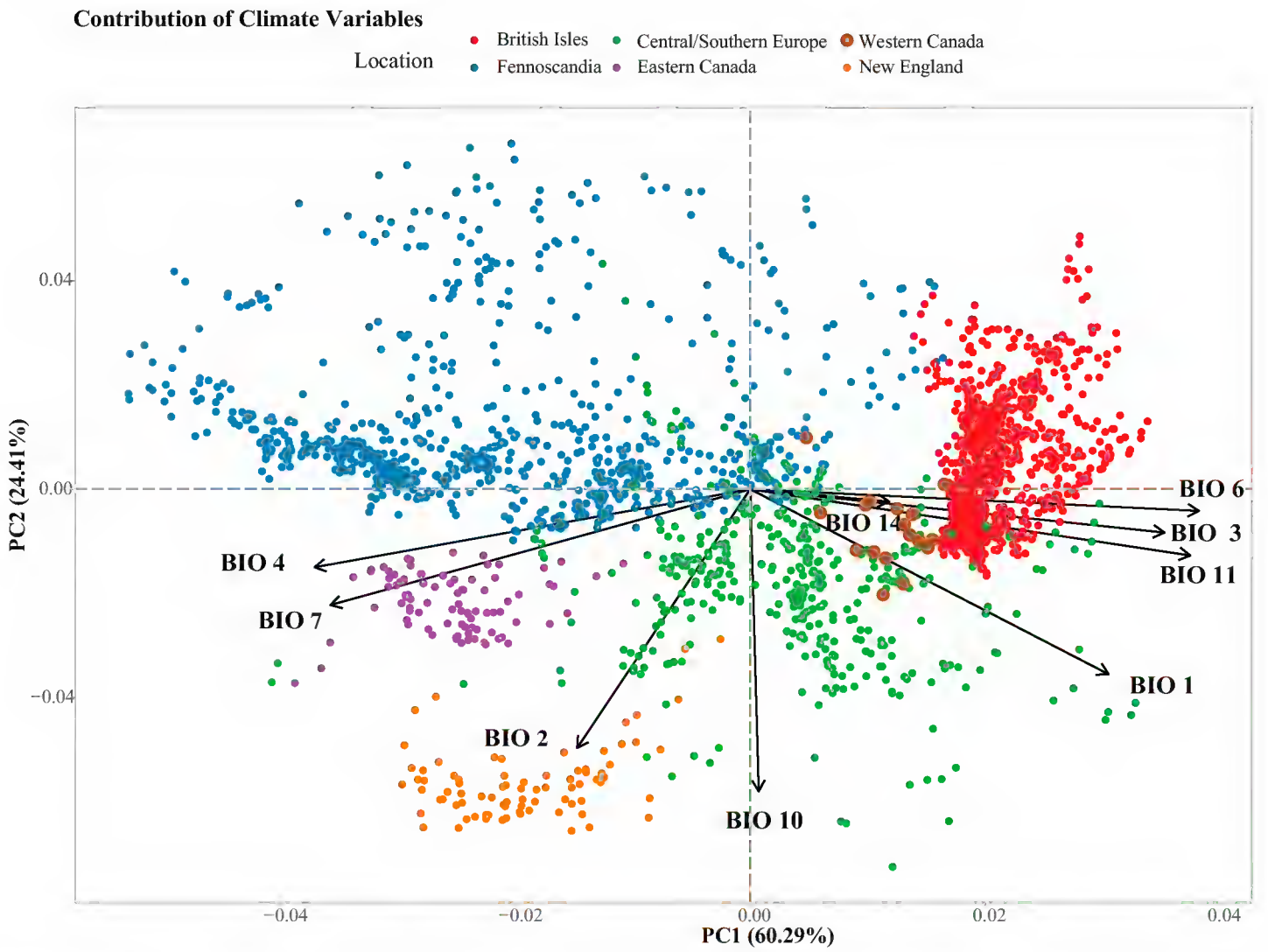


**Figure 5.** Plot of occurrences in each geographic region based on their values for the first two principal component axes derived from values of the nine environmental variables used in the MaxEnt models (Table 1).

North America. There was also some overlap in the distribution of Fennoscandia and Central/Southern Europe. Of all invaded regions, the climate in the New England occurrence locations were generally the most different from climates within the native range.

## Discussion

As expected, each of the three models predicted suitable habitat in portions of Europe from which occurrence data were located (Fig. 2). Averaging predictions across all three models from the native range (Fig. 3A) produces a predicted European range very similar to the range described in Kozhanchikov (1950) (Fig. 1), though the model fails to predict suitable habitat in Ukraine and southeastern Russia. However, the lack of predicted presence in these areas could have arisen simply from inadequate sampling in that region. Winter moth was recently reported from Tunisia (Mannai et al. 2015), and genetic analyses suggest this population is native to the region (Andersen et al. 2019b). Andersen et al. (2019b) also reported winter moth occurrence in southern Spain and Italy. Because dates of these observations fall outside of the range of dates that were used for the climate data (1970–2010), they were not used in our analysis,

though their inclusion could further change the predicted distribution of winter moth to include additional Mediterranean locations. The species is also reported as an established non-native species in Iceland (Halldórsson et al. 2019).

The average of predictions from the models based on the three native range regions predicts suitable habitat in northwestern Washington, along the coast of Western Canada and northward along the coast into Alaska (Fig. 3B). Though winter moth has been established in part of this region (i.e. coastal British Columbia) for over 50 years it has not spread into most of the predicted region. It is possible that populations in this region are constrained from expanding into a climatically suitable region by a biotic factor, such as the introduced parasitoid *Cyzenis albicans* (Elkinton et al. 2015; Roland and Embree 1995), other natural enemies (Broadley et al. 2019) though there are only a few examples where natural enemies are known to constrain the range of an insect species (e.g., Elkinton et al. 2006, Parry 2008). Another possibility is that hybridization with the native congener, Bruce spanworm (Andersen et al. 2019a) alters the fitness of invading populations, thereby constraining their range. Predictions of the model appear to align with invaded portions of Eastern North America more poorly. The model predicts most of the invaded portions of Nova Scotia and New England as low suitability but classifies all of Newfoundland and portions of Labrador, areas that have never been invaded, as either low or medium suitability. However, it is possible that winter moth has never had the opportunity to invade these regions since the Gulf of St. Lawrence separates them from the currently invaded area. As stated earlier, this lack of agreement in portions of the Eastern North America between the model and winter moth occurrence could also be due to hybridization with Bruce spanworm (Havill et al. 2017).

Predictions of suitable habitat based on climatic niche models fit to native occurrence records sometimes do not coincide well with actual invaded regions (Broennimann et al. 2007; Jiménez-Valverde et al. 2011; Ørsted and Ørsted 2019; Roura-Pascual et al. 2006; Steiner et al. 2008), and this may result from factors such as species not being in equilibrium with the local climate, release from competitors and predators, or sampling and dispersal limitations. Fitzpatrick et al. (2007) found similar results of under-predicting the invasive potential of fire ants using native range occurrence records and over-predicting the southern boundary of the native range using invaded range records, which they concluded was due to fire ants establishing in a novel environment similar to their native environment and then expanding into novel climatic environments not available in their native range.

It is not unusual for populations of various species to become locally adapted to their climate and such local adaptation can result in variation in the potential alien range of populations originating from different portions of the native range. In such cases, models built with spatially partitioned occurrence records from the native range may provide some indication of the geographic origins of invaded populations (Steiner et al. 2008). However, without prior knowledge of the extent of local adaptation, such reconstruction of the origins of invading populations may not be possible. In our analysis, models based on records from all three native regions predict suitability in the western Canada invaded range near Vancouver and Victoria (Fig. 2). Analysis of

climatic conditions (Fig. 5) indicates considerable overlap in climate between invaded areas of Western Canada and all three native regions. Thus, our analysis does not show any uniquely high similarity of the invaded portion of Western Canada with any single region of Europe. Only two models fit to European regions (Fennoscandia and the Central/Southern Europe) show suitable habitat in Nova Scotia. In the ridgeline plots (Fig. 4) and the PCA plots (Fig. 5) the records from Eastern Canada fall closest to those of Fennoscandia, suggesting this region as a possible origin for the Eastern Canada population. The model fit to the Central/Southern Europe occurrence records is the only model that predicts suitable habitat in New England, specifically near Cape Cod. When plotting climatic conditions using PCA (Fig. 5), the New England records appear to occupy a different niche mainly outside of the distribution of records from all other regions, though perhaps most similar to the Central/Southern Europe native region, supporting the hypothesis of that region being the origin of the invasion. However, we have no evidence of local adaptation to climate in the winter moth's native range, so such attribution is tentative.

Adaptation to local environments is often observed in species with large geographical ranges (Osborne and Suárez-Seoane 2002; Peterson and Vargas 1993). Differences in predictions from models based on native range occurrence records are apparent in AUC scores (Table 2), the variables of greatest contribution (Table 2) and the averaged prediction (Fig. 3). Probabilities averaged across the three models based on native range regions accurately predicted suitable North American habitat in most of the invaded regions, but predicted particularly high habitat suitability in invaded portions of the south coast of British Columbia (Fig. 3). However, it also predicted large areas of medium to high habitat suitability in uninvaded regions north of both the western and eastern invaded regions. It is suggested that distribution models may be useful in predicting regions where species are likely to invade, but may be flawed in predicting subsequent spread in novel regions (Fitzpatrick et al. 2007; Loo et al. 2007). Given that many of the large areas of predicted suitable habitat are adjacent to currently invaded areas but remain uninvaded, we suspect that there may be unknown biotic or abiotic factors (other than the climatic variables considered here) that limit North American populations into these northern uninvaded areas. However, the identity of such biotic factors remains unknown and we encourage further research into the biotic variables that may be limiting the spread of winter moth in its invaded regions.

## Conclusions

We focused our study on a generalist herbivore, the winter moth, to predict areas in North America where this species is likely to invade. We applied MaxEnt, the most widely used species distribution and niche modelling algorithm, to predict the potential range of suitable habitat for winter moth. Preliminary model runs fit to large re-

gions of winter moth occurrence highlighted a high sampling bias in the United Kingdom. We implemented a simple method of applying spatial filters based on geography to reduce sampling bias. Environmental variables were selected based on expectations of climatic factors likely to be important to the biology of this species. We chose to use environmental variables at a coarse grain (25 km) due to the widespread nature of this species and multi-continental areas of interest.

Differentiating the geographic origins for each of the North American winter moth ranges based on predictions from the various native geographic bins is possible, assuming local adaptation to climate in native populations. Based upon climatic similarity, central Europe appears to be the most likely origin of non-native populations in New England. Climatic similarity of the invaded range in Eastern Canada with Fennoscandia and Central Europe suggests those regions as likely origins. However, the Western Canada invaded range appeared equally similar to all native regions and thus there was no evidence regarding possible origins. All of these conclusions regarding origin remain speculative and would require confirmation based on genetic similarities. Combining molecular marker studies in ecological niche modelling approaches can help advance this field (Scoble and Lowe 2010) and improve future predictions of species distribution trajectories. Furthermore, evidence of hybridization with the native Bruce spanworm has been shown in New England, Oregon, British Columbia and Nova Scotia (Andersen et al. 2019a; Elkinton et al. 2010; Havill et al. 2017). If alleles from Bruce spanworm can introgress into winter moth, then this hybridization may increase winter moth's ability to adapt to a novel environment, leading to a shift in the species' fundamental niche (Holt and Gaines 1992).

Predicting the potential North American distribution of this invasive species can aid managers in proactively selecting survey locations for this destructive moth. Areas outside the current species' distribution, which are highly suitable for winter moth, may be prioritized for biosecurity measures to help prevent establishment of this species. However, it remains to be confirmed whether winter moth could establish in the vast regions predicted to be suitable north of currently invaded areas. Given that winter moth is not currently expanding its range into these areas, many of which are adjacent to currently invaded regions, there may be unknown biotic factors that limit the range of this species in ways that are not currently understood.

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